生物量分配影响三种不同海拔起源的松树生长 *

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摘要：松属的思茅松（*Pinus kesiya* var. *langbianensis*）、云南松（*P. yunnanensis*）和高山松（*P. densata*）是组成中国西南不同海拔针叶森林的主要树种，然而这三个树种在发育速度尤其是高生长方面表现出明显的差异。为了弄清引起这些变异的生理和形态学原因，本文将三种松树种植于同一环境下，对其光合作用、生物量分配、生长速率和叶片性状进行了研究。研究发现，与来源于高海拔的树种相比，低海拔的树种有更高的株高、以及更大的干物质重量、相对生长速率、叶质比、茎质比和比叶面积，但叶片氮含量、碳含量和根质比较低。高海拔树种的光合速率并不明显低于低海拔树种。相对生长速率和树高均与叶质比呈显著正相关，与根质比负相关，但与最大光合速率没有显著关系。这些结果表明，生物量的分配式样和长期的形态特性能够更好地预测不同海拔松树的生长表现。

关键词：生物量分配；海拔；生长；光合作用；松树

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Biomass Partitioning Affects the Growth of *Pinus* Species from Different Elevations

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Abstract：The conifer forests in southwestern China are mainly dominated by three vicariant species within *Pinus*：*P. kesiya* var. *langbianensis*，*P. yunnanensis*，and *P. densata*. Their sites range from lower to higher elevations，respectively，and each species shows differences in rates of development，especially with regard to height. To identify the physiological and morphological causes of this inherent variation，photosynthesis，biomass partitioning，growth rates and leaf traits were investigated of plants cultivated under the same environmental conditions. Trees of the species native to the lower elevation were taller，and had higher values for dry weight，relative growth rate（RGR），leaf mass fraction（LMF），stem mass fraction（SMF），and specific leaf area per unit mass（SLA），relative to those from the higher elevations. However，their leaf N and C contents per unit area，and their root mass fraction（RMF），were smaller than those of high-elevation trees. Photosynthetic capacity in species from high elevations was not significantly reduced from the level calculated for trees from lower elevations. Both RGR and tree height were positively correlated with LMF and negatively with RMF，but no significant positive correlations were found with maximum photosynthetic rate determined on both an area-basis（A_{max}）and mass-basis（A_{mass}）. These findings suggest that the patterns of biomass partitioning and long-term morphological traits are better predictors of performance among trees of different *Pinus* species growing along an elevational gradient.

Key words：Biomass partitioning；Elevation；Growth；Photosynthesis；*Pinus*

Wide variations in growth rates among trees across species are closely correlated with investments of carbon resources and ecological distributions (Wright and Westoby, 2000; Poorter and Garnier, 2007; King et al., 2013). Fast-growing species are generally found in relatively more fertile habitats, whereas species that occupy infertile environments tend to have low growth rates (Biere, 1996; Poorter and Garnier, 2007). Those rates can affect seedling survival, reproduction, productivity, competition, and forest structures (Lambers and Poorter, 1992; Biere, 1996; Coomes and Allen, 2007). Therefore, examining the factors that influence tree growth is essential for modeling forest productivity and its functioning under climatic change (Coomes and Allen, 2007; King et al., 2013).

Relative growth rate (RGR) is a complex trait that is determined by differences in physiology, morphology, and biomass partitioning (Shipley, 2006; Poorter and Garnier, 2007; Poorter et al., 2012). This trait encompasses three variable components: net assimilation rate (NAR), specific leaf area (SLA), and leaf mass ratio (LMR) (Poorter and Garnier, 2007; Poorter et al., 2012; Tomlinson et al., 2012). For example, species from humid environments partition more biomass to the roots and less to the stems than those from semiarid environments in Australia, Africa, and South America (Tomlinson et al., 2012). Poorter and Remkes (1990) have found, in a controlled experiment, that the RGRs of 69 plant species are most strongly correlated with SLA and LMR, but are also positively associated with biomass allocation to the leaves and NAR. However, based on the results of a meta-analysis with 614 species from 83 different experiments in Europe, America, and Australia, Shipley (2006) has suggested that LMR is never strongly related to RGR but, instead, NAR is the best general predictor of variations in interspecific RGRs. Consequently, the relative contribution of SLA, NAR, and LMR to RGR varies among species or when plants are grown in contrasting environments.

Trees in the *Pinus* genus cover a large geographical area and a wide variety of habitats in southwestern China, where they are of great economic and ecological importance. As the dominant component of conifer forests in that region, the three vicariant species, from low to high elevation, are *P. kesiya* Royle ex Gordon var. *langbianensis* Gaussen, *P. yunnanensis* Franch., and *P. densata* Mast. (Wu, 1990). These species exhibit different rates of development in their habitats, especially in height increment, with *P. kesiya* being the fastest grower (Dai et al., 2006). However, the physiological and morphological causes underlying those differences are not completely known.

Plant heights and biomass production in trees generally decline with increasing elevation, as shown in both common garden studies and natural forests (Oleksyn et al., 1998; Li et al., 2003; Coomes and Allen, 2007). However, the extent of the correlation between elevation and annual stem elongation can differ among species (Angert, 2006). For example, highland plants might display slower growth rates because of morphological or physiological reasons (Atkin et al., 1996a; Oleksyn et al., 1998; Angert, 2006). Hoch et al. (2002) have suggested that a low temperature-driven sink explains the lag in growth by *P. cembra* at higher elevations at the tree line in the Swiss Alps. Although some studies demonstrated that leaf thickness, leaf N content, and photosynthetic rates are greater in highland plants than in lowland plants on the island of Hawaii or the Northern America continent (Cordell et al., 1999; Hultine and Marshall, 2000), conflicting results from other investigations shown that a general trend in photosynthetic capacity does not occur across elevations in the tropical high Andes and southwest China (Cabrera et al., 1998; Zhang et al., 2007; 2011). For example, clones of spruce from the tree line have a 4.3-fold lower growth rate and they contain 60% less chlorophyll per unit mass than trees from valleys in Europe (Polle et al., 1999). Westbeek et al. (1999) have reported, from a common garden, that RGR is negatively correlated with leaf N content per unit area, as

well as with chlorophyll and Rubisco contents, for *Poa* species in both alpine and lowland regions. Despite greater photosynthetic rates in high-elevation populations, seedling heights and dry masses measured in common garden studies decline with the elevation at which their seed originated. Proportional dry mass partitioning in the roots nearly doubles with increasing elevation of origin in controlled experiments (Oleksyn *et al.*, 1998). Consequently, researchers still do not have a clear understanding of the causes for low relative growth rates by highland plants.

Here, the growth rates, leaf N contents, specific leaf areas, biomass partitioning, and photosynthetic rates of *P. kesiya*, *P. yunnanensis* and *P. densata* were monitored in a common garden at Kunming Botanical Garden, China. The objective was to identify the factors affecting the development of pines that originate from different elevations. We hypothesized that there is an inherent difference in the relative growth rate of these three species, and that this difference is correlated with leaf physiology and biomass partitioning.

1　Materials and methods

1.1　Plant species and sites

Three species in *Pinus*—*P. kesiya*, *P. yunnanensis*, and *P. densata*—were selected. All are evergreen species that dominate conifer forests, from low to high elevation, respectively, in southwestern China (Table 1). Seeds of *P. kesiya*, *P. yunnanensis*, and *P. densata* were collected from Puwen (elev. 1 377 m), Jianchuan (2 196 m), and Deqing (3 447 m), respectively, from October to December in 2006. They were sown at Kunming Botanical Garden (elev. 1 990 m; E 102.74°, N 25.15°) on 22 March 2007 and had germinated by 9 April. 70 seedlings per

species were transplanted on 7 May into plastic pots filled with a peat, forest soil, and humus mixture (1∶3∶1; v∶v∶v). The initial dry mass of sample seedlings from each species was measured 1 d before transplanting occurred, and the final harvest was made on 12 October 2007. After transplanting, the seedlings were grown under full sunlight, and were fertilized monthly with a liquid nutrient solution and watered every 2 to 3 d. From May to October, the mean monthly temperature ranged from 13.2 ℃ to 19.9 ℃ (mean ± *SD*, 17.6 ± 2.4 ℃) while mean monthly precipitation was 19.6 mm to 204.0 mm (mean ± *SD*, 115.7 ± 74.6 mm).

1.2　Physiological measurements

Gas exchange in response to light and CO_2 concentration was recorded on 7 to 9 October 2007 from fully expanded leaves, using a LI-6400 portable photosynthesis system (LI-COR, Lincoln, NE, USA). Data were recorded from 10 plants per species. Before the measurements began, each sample leaf was exposed to actinic light of 1 200 μmol m^{-2}s^{-1} (10% blue, 90% red) for 15 min to induce maximum stomatal opening. Curves for the photosynthetic light response (*A*-PPFD) were made using an automated protocol built into the LI-6400. The program was configured to advance to the next step if the sum of three coefficients of variation (CO_2, water vapor, and flow rate) was less than 0.3%. The minimum waiting time was 3 min. Each leaf was equilibrated to initial conditions by waiting at least 15 min before executing the automated protocol. *A*-PPFD curves were generated for 6 leaves per species, at light intensities of 2 000, 1 600, 1 200, 1 000, 800, 600, 400, 300, 200, 100, 50, and 0 μmol m^{-2}s^{-1}. Other test conditions included a controlled level of CO_2 (380 μmol mol^{-1}), a flow rate of 500 μmol s^{-1}, a

Table 1　Origins of the three *Pinus* species used in this study

Species	Code	Elevation range/m	Site for seed collection		
			Longitude	Latitude	Elevation/m
P. kesiya	Pk	600−1600	E100°55′	N22°22′	1377
P. yunnanensis	Py	1000−3200	E99°54′	N26°32′	2196
P. densata	Pd	2600−3600	E98°52′	N28°27′	3447

leaf temperature of 25 ℃, and a vapor pressure deficit (VPD) of 0.6 to 1.0 kPa.

Photosynthetic CO_2 response curves (A-C_i) and A-PPFD curves were determined for the same leaves. After measurements were completed for the A-PPFD curve, each leaf was exposed for 15 min to a light intensity of 1 200 μmol m^{-2}s^{-1} and a CO_2 concentration of 380 μmol mol^{-1}. Other conditions were a leaf temperature of 25 ℃ and VPD of 1.0 to 1.5 kPa. The A-C_i curve measurement was started at ambient CO_2 concentration, which decreased gradually to 0 μmol mol^{-1}, returned to 380 μmol mol^{-1}, and then increased to a higher concentration to ensure that the stomata remained open throughout the recording period. Photosynthetic rates were measured at different CO_2 concentrations, using the automated protocol built into the LI-6400.

After completing the gas exchange measurements, we recalculated the photosynthetic rate based on actual leaf area values, which were estimated by the method of Johnson (1984):

$$LA = 2L(1 + \pi/n) \sqrt{(nv/\pi L)} \qquad (1)$$

where LA is leaf area (cm^{-2}), L is needle length (cm), n is the number of needles per fascicle (n = 3 for *P. kesiya* and *P. yunnanensis*; n = 5 for *P. densata*), and needle volume (v) is estimated via water displacement (Johnson, 1984).

Photosynthetic light response curves were fitted with non-rectangular hyperbola. The maximum photosynthetic rate (A_{max}) and respiration rate (R_d) were determined via Photosyn Assistant v1.1 (Dundee Scientific, Dundee, Scotland, UK) according to the method of Prioul and Chartier (1977). Using A-C_i curves, we calculated the maximum carboxylation rate by Rubisco (V_{cmax}) and light-saturated electron transport (J_{max}) with Photosyn Assistant, based on the photosynthetic model of von Caemmerer and Farquhar (1981).

Mesophyll diffusion conductance (g_m) from the internal air space to the chloroplasts was estimated according to the method of Harley *et al*. (1992):

$$g_m = \frac{A}{C_i - \dfrac{\Gamma^* [J_{max} + 8(A + R_d)]}{J_{max} - 4(A + R_d)}} \qquad (2)$$

where the value for R_d is found from the A-PPFD curve, and Γ^* is the hypothetical CO_2 compensation point in the absence of R_d (42.75 μmol mol^{-1} at 25 ℃) (Bernacchi *et al*., 2001). Values for g_m were calculated from our measurements of photosynthesis at internal CO_2 concentrations of 100 to 300 μmol mol^{-1}, with the average value of g_m being determined for each leaf.

Chlorophyll was extracted per the technique of Moran and Porath (1980), and its concentration was analyzed on a UV-2550 spectrophotometer (Shimadzu, Japan) before being calculated according to the equations of Inskeep and Bloom (1985).

1.3　Growth rate and biomass partitioning

After the photosynthetic data were obtained, the plants were harvested and divided into root, stem, and leaf portions. Ten plants were measured for each species. The dry mass of each portion was recorded after the tissues were dried for 48 h at 80 ℃. Afterward, the leaf mass fraction (LMF), stem mass fraction (SMF), and root mass fraction (RMF) were determined in proportion to total dry mass per plant. The values for relative growth rate were calculated by the following formula (Poorter and Garnier, 2007).

$$RGR = \frac{\ln M_2 - \ln M_1}{t_2 - t_1} \qquad (3)$$

where M_1 and M_2 are the biomass at time t_1 and t_2, respectively; and $t_2 - t_1$ is the time span between measuring events. Here, that span was 185 d.

Leaf area per plant was determined according to the method of Johnson (1984). From this, SLA was calculated as the specific leaf area per unit mass (m^2 kg^{-2}). Leaf N content was assessed with a Leco FP-428 nitrogen analyzer (Leco Corporation, St. Joseph, MI, USA).

1.4　Statistical analysis

Statistical analysis was performed with SPSS 13.0 (SPSS Inc., Chicago, IL, USA). We used one-way ANOVA and LSD multiple comparison tests to esti-

mate the differences in RGR, biomass partitioning, physiological parameters, and leaf N content. Relationships between RGR and leaf traits were assessed through Pearson's regression analysis. A principal component analysis (PCA) was performed to characterize the associations among 17 leaf traits.

2   Results

2.1   Interspecific variations in growth, biomass partitioning, and physiology

Tree height (H) and dry mass per plant varied significantly across species (Fig. 1). For example, plants of *P. kesiya* were taller than those of *P. yunnanensis* and *P. densata* ($P<0.001$) whereas the mean basal diameter from *P. yunnanensis* (1.179±0.140 cm) was larger than from *P. densata* (0.747±0.073 cm). However, the dry mass per plant and the RGRs of *P. kesiya* and *P. yunnanensis* were greater than those of *P. densata* (Fig. 1). Consequently, species from the lower elevations grew more rapidly than the one

from the highest elevation.

Biomass partitioning to the organs also differed significantly among species (Fig. 1). Whereas the fractions of dry matter produced in the leaf and stem were higher in *P. kesiya* and *P. yunnanensis* than in *P. densata*, the root mass fraction showed an opposite trend.

Significant differences among species were found for the area-based respiration rate (R_d) and stomatal conductance (g_s), but not for the area-based photosynthetic rate (A_{max}), mass-based photosynthetic rate (A_{mass}), mass-based respiration rate ($R_{d\text{-}mass}$), maximum carboxylation rate (V_{cmax}), light-saturated electron transport rate (J_{max}), and mesophyll conductance (g_m) (Fig. 2).
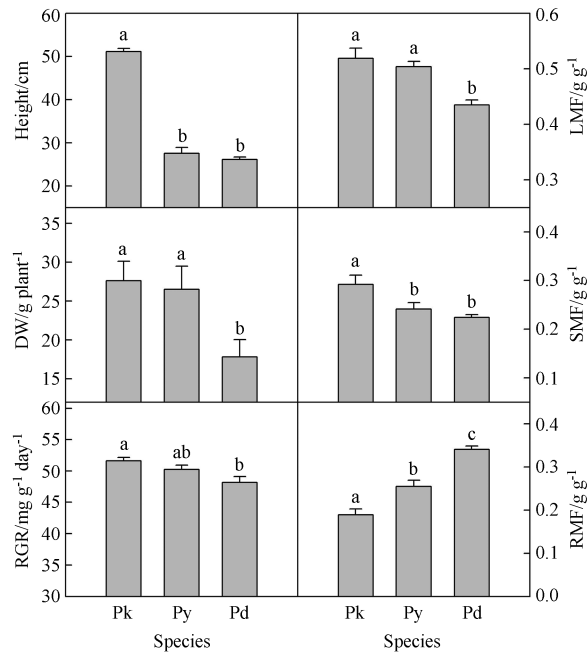

Fig. 1   Differences in plant height, dry mass weight (DW), relative growth rate (RGR), leaf mass fraction (LMF), stem mass fraction (SMF), and root mass fraction (RMF) for *Pinus kesiya* (Pk), *P. yunnanensis* (Py), and *P. densata* (Pd) grown under the same environmental conditions. Different letters above bars for each component indicate statistically significant differences in mean values ($P \leqslant 0.05$), as determined by LSD multiple comparison tests
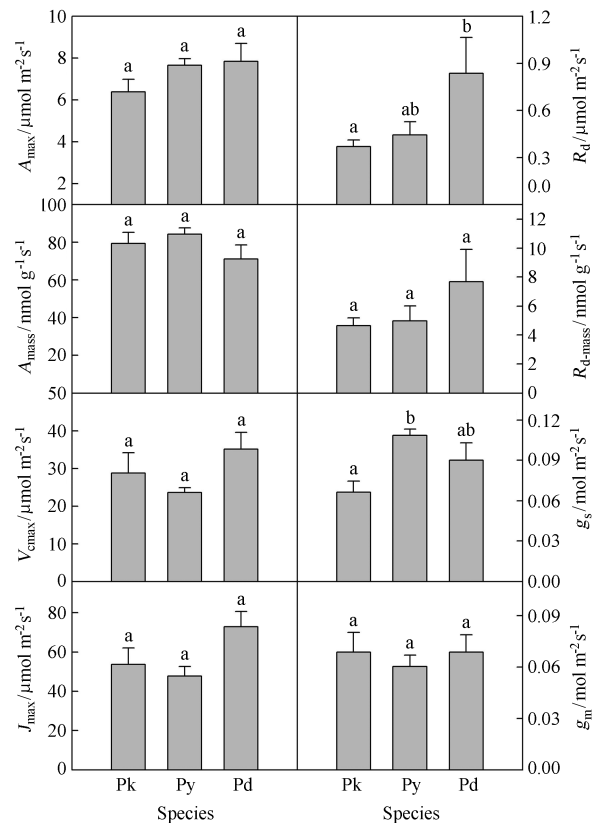

Fig. 2   Comparisons of area-based photosynthetic rate (A_{max}), mass-based photosynthetic rate (A_{mass}), maximum carboxylation rate (V_{cmax}), light-saturated electron transport rate (J_{max}), area-based respiration rate (R_d), mass-based respiration rate ($R_{d\text{-}mass}$), stomatal conductance (g_s), and mesophyll conductance (g_m) among *Pinus kesiya* (Pk), *P. yunnanensis* (Py), and *P. densata* (Pd). Different letters above bars for each component indicate statistically significant differences in mean values ($P \leqslant 0.05$), as determined by LSD multiple comparison tests

Specific leaf area per unit mass (SLA) was lower in species from the higher elevation, but no significant difference in chlorophyll content was detected among species (Fig. 3). Both leaf N content and C content per unit area increased generally with elevation (Fig. 3). However, the mass-based N contents did not differ significantly among species.
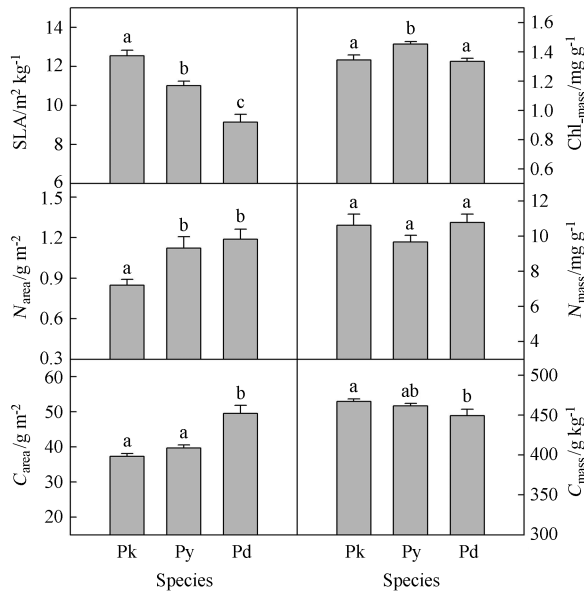

Fig. 3　Differences in specific leaf area (SLA), chlorophyll content per unit mass (Chl$_{\text{-mass}}$), leaf N contents on area-basis (N_{area}) and mass-basis (N_{mass}), and leaf C contents on area-basis (C_{area}) and mass-basis (C_{mass}) from *Pinus kesiya* (Pk), *P. yunnanensis* (Py), and *P. densata* (Pd). Different letters above bars for each component indicate statistically significant differences in mean values ($P \leqslant 0.05$), as determined by LSD multiple comparison tests

2.2　Determinants of growth rate

Tree height was correlated significantly and positively with LMF, SMF, SLA and RGR, but negatively with RMF (Fig. 4). No significant correlation existed between H and A_{max}.

Dry weight per plant was correlated positively with LMF but negatively with RMF. Neither R_{d} nor A_{max} was correlated with dry weight (Fig. 5). RGR was significantly and positively correlated with LMF but negatively with RMF. No significant correlations were found between RGR and A_{max} or A_{mass} (Fig. 6). Finally, A_{max} was positively correlated with V_{cmax}, J_{max}, g_{s}, g_{m}, and leaf N content per unit area, but negatively with SLA (data not shown).
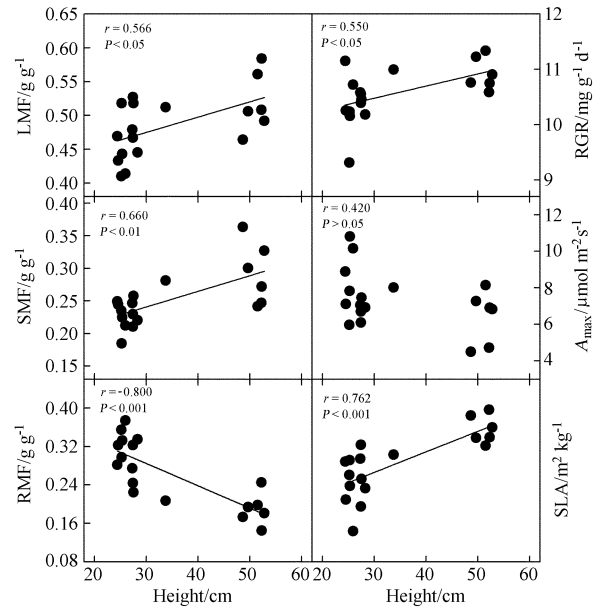

Fig. 4　Pearson correlations of plant height with leaf mass fraction (LMF), stem mass fraction (SMF), root mass fraction (RMF), relative growth rate (RGR), maximum photosynthetic rate (A_{max}), and specific leaf area (SLA) for 3 *Pinus* species
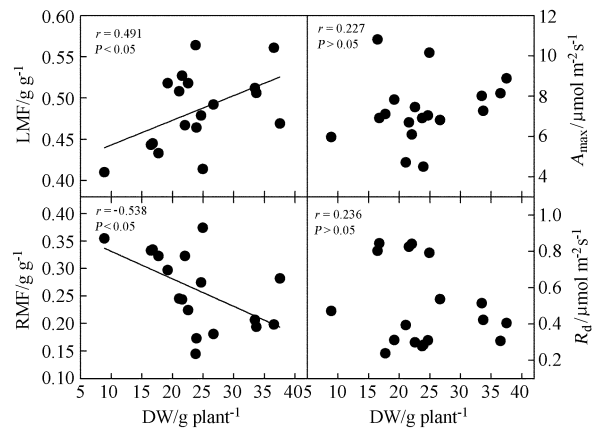

Fig. 5　Pearson correlations of dry mass weight (DW) with leaf mass fraction (LMF), root mass fraction (RMF), maximum photosynthetic rate (A_{max}), and respiration rate (R_{d}) for 3 *Pinus* species

Principal component analysis showed that H, RGR, LMF, RSF, RMF, and SLA loaded mainly on the first PCA axis, explaining 36.6% of the total variation; A_{max}, J_{max}, V_{cmax}, g_{s}, g_{m}, and leaf N content per unit area (N_{area}) loaded on the second axis, explaining 26.3% of the total (Fig. 7). The first axis of the PCA was mainly associated with plant growth and biomass partitioning while the second axis was associated with photosynthetic carbon assimilation.
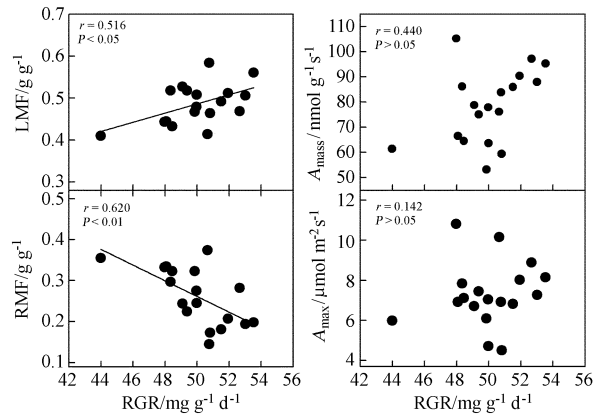
Fig. 6 Pearson correlations of relative growth rate (RGR) with leaf mass fraction (LMF), root mass fraction (RMF), mass-based maximum photosynthetic rate (A_{mass}), and area-based maximum photosynthetic rate (A_{max}) for 3 *Pinus* species
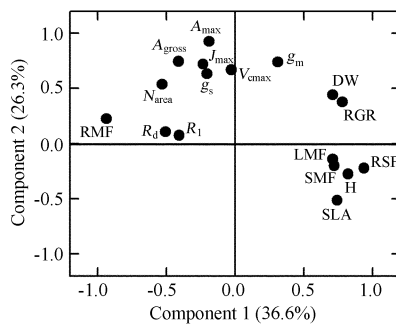

Fig. 7 Principle component analysis of 17 leaf traits from 3 *Pinus* species. A_{gross}, gross photosynthetic rate; A_{max}, area-based maximum photosynthetic rate; DW, dry mass weight per plant; g_m, mesophyll conductance; g_s, stomatal conductance; H, tree height; J_{max}, light-saturated electron transport rate; LMF, leaf mass fraction; N_{area}, nitrogen content per unit area; R_d, dark-respiration rate; RGR, relative growth rate; RMF, root mass fraction; R_l, photorespiration rate; RSF, root-shoot ratio; SLA, specific leaf area per unit mass; SMF, stem mass fraction; V_{cmax}, maximum carboxylation rate

3　Discussion

3.1　Growth rate in relation to elevation

Seedlings of *Pinus* species originating from the highest elevation were shorter and had smaller values for RGR than congeneric species from the lowest elevation. This indicated that the former grew more slowly. These findings are in line with previous reports from common gardens and natural forests that tree height and biomass production are reduced as elevation increases (Oleksyn et al., 1998; Li et al., 2004; Coomes and Allen, 2007). Li et al. (2003) have found that the mean annual biomass increment

per tree in the eastern Himalayas is less as elevation increases, i.e., reduced by 476 g per 100 m between 1 680 and 1 810 m and by 103 g between 1 810 and 1 940 m. However, Angert (2006) has shown in common garden experiments that trees within a given species accumulate their greatest aboveground biomass when grown under a temperature regime that is characteristic of the center of its natural elevation range. Thus, the effect of seed origin or elevation on RGR is considered species-specific (Angert, 2006).

3.2　Growth rate in relation to biomass partitioning

The decline in growth rate with increasing elevation can be caused by both environmental and genetic factors (Körner, 2003; Li et al., 2003; King et al., 2013). For example, in natural forests, a shorter growing season that results from low temperatures at a higher elevation can reduce a tree's accumulation of C and its growth rate (Oleksyn et al., 1998; Körner, 2003). Because seeds of the trees used in our study were collected at different elevations but were then exposed to the same experimental conditions, any interspecific variations in tree growth rates would have reflected inherent genetic differences.

Present study demonstrated that tree height, dry weight, and relative growth rate were correlated positively with the leaf mass fraction, but negatively with the root mass fraction. Previous studies under controlled conditions have also revealed that RGR is positively associated with biomass partitioning in the leaves (Poorter and Remkes, 1990; Wright and Westoby, 2000). By contrast, Shipley (2006) has noted no significant correlation between RGR and LMF in 83 different experiments. The essential resources needed by plants are acquired by different organs; more resources allocated to the leaves can increase light capture, while more resources transported to the roots can improve the uptake of water and mineral elements (Taub, 2004). Because plants are composed largely of materials derived via photosynthesis, an increased partitioning to non-photosynthetic organs would reduce their growth rate in general (Mooney, 1972). Consequently, the functional balance between

leaves and roots is an important determinant of inter-specific differences in RGR (Wright and Westoby, 2000; Osone *et al.*, 2008).

Biomass partitioning in different organs may reflect a survival strategy that is adjusted to meet current environmental conditions (Poorter *et al.*, 2012). The process of allocating C to either the roots or shoots is more sensitive to temperature, shade, and water deficit (Poorter *et al.*, 2012; Tomlinson *et al.*, 2012). Generally, plants in cold environments tend to accumulate more dry matter in the roots, boosting their production of those tissues (Oleksyn *et al.*, 1998; Li *et al.*, 2004), while also reducing their stem and leaf fractions to increase RMF values (Poorter *et al.*, 2012). Plants that decrease the proportion of leaves and partition more biomass to their roots at higher elevations or on less productive sites will benefit from faster recovery of their growth rates the following year, and will be better able to adapt to unfavorable climatic conditions (Oleksyn *et al.*, 1998; Körner, 2003). However, improved survivability comes at the expense of slower growth because plants must respond to environmental gradients by adjusting their pattern of partitioning biomass to maximize growth performance (Wang *et al.*, 2008).

3.3　Correlation of growth rate with photosynthetic rate

Maximum photosynthetic rate was not correlated with tree height, plant dry weight, or RGR in our three *Pinus* species. These results contradict previous findings from controlled experiments that RGR is correlated with the photosynthetic rate (Lambers and Poorter, 1992; Atkin *et al.*, 1996b; Shipley, 2006). Villar *et al.* (2005) have also suggested that RGR is correlated with NAR during a short growing period, but with morphological traits over the long term. However, maximum photosynthetic rates for the three species did not vary with elevation, but were positively correlated with CO_2 diffusive conductance and leaf N content per unit area while negatively correlated with SLA. Earlier researchers have implied that no general trend in photosynthetic rate and leaf traits exists across elevations in natural habitats (Cabrera *et al.*, 1998, Zhang *et al.*, 2007; 2011). Villar *et al.* (1998) have suggested that the photosynthetic rate in *Aegilops* species is negatively correlated with SLA in a common garden, thereby accounting for the absence of a correlation between SLA and RGR.

In conclusion, the pines grown from seed gathered at higher elevations had slower growth rates, but their photosynthetic capacity was not significantly inferior to that of trees representing lower elevations. We believe that, at higher elevations, plants tend to allocate more biomass to the roots while reducing their leaf production, which ultimately leads to slower growth. The pattern of biomass partitioning, rather than photosynthetic capacity, determines any interspecific variations in growth rates among *Pinus* species originating from different elevations. Thus, long-term morphological traits are better predictors of growth rates for trees along an elevational gradient.

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